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Seasonality of reproduction in Asian elephants *Elephas maximus* and African elephants *Loxodonta africana*: underlying photoperiodic cueing?

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Für meine Eltern, die mich immer unterstützt haben

INHALTSVERZEICHNIS

Vetsuisse Faculty University of Zurich (2018)

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Seasonality of reproduction in Asian elephants *Elephas maximus* and African elephants *Loxodonta africana*: underlying photoperiodic cueing?

Long-lived mammals relying on seasonal food sources often have reproductive cycles controlled by photoperiod and either are classified as short-day breeders or long-day breeders. The evolutionary history of elephants probably included an adaptation to seasonal environments, as *Elephas* species ventured into Europe, and the historical distribution of both *Loxodonta* and *Elephas* spread beyond the tropics, respectively. Assuming that birth in spring (during the long-day period) is desirable and based on their long gestation length of nearly two full years, one might expect elephants to breed seasonally with increased breeding activity in the long-day period. Many elephants kept in zoos face reproductive problems; especially acyclicity as an increasing issue. While the majority of publications on zoo elephants focus on acyclicity and potential causes, no treatment of the relevance of seasonal reproduction or photoperiodic cueing in elephants exists, to our knowledge. We reviewed the literature on the seasonality of reproduction in free-ranging Asian and African elephants and evaluated data on seasonality in captive populations, assessing potential photoperiodic cueing. Additionally, we reviewed literature on other factors affecting reproduction in free-ranging and captive populations, including environmental conditions, social intraspecific interactions and human management.

Keywords: breeding, elephant, long-day breeder, photoperiod, season

Vetsuisse-Fakultät Universität Zürich (2018)
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Langlebige Säugetiere, welche von saisonalem Nahrungsvorkommen abhängig sind, haben oft Reproduktionszyklen welche durch Photoperiodismus kontrolliert werden, und werden entweder als „short-day breeder“ (Kurztag) oder „long-day breeder“ (Langtag) eingeteilt. Die evolutionäre Geschichte von Elefanten hat wahrscheinlich auch eine Anpassung an saisonale Umwelteinflüsse beinhaltet. Angenommen, eine Geburt im Frühling (in der Langtag-Phase) ist erstrebenswert und aufgrund der langen Tragzeit von fast zwei Jahren, wäre es wahrscheinlich, dass sich Elefanten saisonal paaren mit erhöhter Paarungshäufigkeit in der Langtag-Phase. Viele Elefanten in Zoos zeigen Reproduktionsschwierigkeiten; vor allem Azyklie ist ein immer häufigeres Problem. Während sich die Mehrheit der Publikationen über Zooelefanten auf die Azyklie und mögliche Ursachen konzentriert, hat sich unseres Wissens niemand mit Saisonalität und Photoperiodismus bei Elefanten beschäftigt. Wir sind all die Literatur über Reproduktionssaisonalität bei freilebenden Asiatischen und Afrikanischen Elefanten durchgegangen und haben Daten über Saisonalität bei Populationen in Menschenobhut evaluiert, wobei wir versuchten, den Effekt von Photoperiodismus abzuschätzen. Zusätzlich sind wir Literatur über andere Faktoren durchgegangen, welche die Fortpflanzung bei freilebenden Populationen und Populationen in Menschenobhut beeinflussen, wie Umgebungsbedingungen, soziale intraspezifische Interaktionen und menschliches Management.

Schlüsselwörter: Fortpflanzung, Elefant, Langtag-Reproduktion, Photoperiodismus, Saison

MAMMAL REVIEW

Seasonality of reproduction in Asian elephants *Elephas maximus* and African elephants *Loxodonta africana*: underlying photoperiodic cueing?

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Keywords

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ABSTRACT

1. Animals in seasonal environments often rely on photoperiodicity to time their reproduction. Elephants have a gestation length of approximately two years and a historical geographic distribution including higher latitudes than at present, so the evolution of a seasonal breeding pattern cued by photoperiodicity and timed to the long-day period is a theoretical option in both species.
2. We reviewed literature on reproductive patterns in free-ranging, semi-captive and captive Asian and African elephants, photoperiodic cueing, seasonal variation of body condition and other factors influencing their reproduction, as well as data from zoological collections on the timing of births.
3. Most of the free-ranging and all the semi-captive and captive elephant populations showed a moderate yet distinct seasonal breeding pattern.
4. Peak breeding activity of free-ranging Asian elephants took place in either the dry or the wet season, with no preference for short-day or long-day breeding at low latitudes (close to the equator) but a preference for long-day breeding at higher latitudes. Semi-captive Asian elephants mainly bred in the dry season when body condition was lowest and day-lengths were increasing. Peak conception

often occurred in the wet season in free-ranging African elephants when body condition was highest, with no evident preference for short-day or long-day breeding at low latitudes but preference for long-day breeding at higher latitudes.
5. Asian and African elephants in zoos at latitudes from 43 to 53°N tended to conceive more often during spring and summer, i.e. when day-lengths were increasing. Body condition was not reported to vary significantly throughout the year and was rather high compared to in the wild.
6. We hypothesise that elephants are 'long-day breeders' in which the photoperiodic timing of conception can be influenced by many additional factors. Strategies to encourage natural conception in captive populations should include measures aimed at increasing breeding incentives in the northern hemisphere spring.

INTRODUCTION

Long-lived mammals relying on seasonal food sources often have reproductive cycles controlled by photoperiod to ensure birthing during a time of favourable resources (Bronson & Heideman 1994, Bechert et al. 1999). Depending on whether an increase or a decrease in melatonin triggers seasonal reproduction, animals are classified as short-day breeders (autumn/winter) or long-day breeders (spring/summer; viviD & Bentley 2018). Assuming that birth in spring (during the long-day period) is desirable, and knowing the species-specific gestation length (or period), it can be predicted whether a species is a short-day or long-day breeder (Fig. 1). The evolutionary history of elephants probably included a period of adaptation to seasonal environments, as *Elephas* species ventured into Europe (Van der Made & Mazo 2003, Van der Made 2010), and the historical distribution of both *Loxodonta africana* and *Elephas maximus* spread beyond the tropics of capricorn and cancer, respectively (Laursen & Bekoff 1978, Shoshani & Eisenberg 1982). Based on their long gestation length of nearly two full years (Lüders 2018), one might therefore expect them to increase breeding activity in the long-day period (Fig. 1).

Many elephants kept in zoos face reproductive problems. In both species, pathologies of ovarian and uterine origin are common, as is continuous cyclicity due to a lack of breeding; acyclicity is an increasing issue, especially in reproductive-aged African females, whereas Asian females often cease reproductive activity early in life and suffer from reproductive tract pathologies affecting fertility (Dow et al. 2011, Hildebrandt et al. 2012, Brown 2014, Brown et al. 2016). Another problem is high infant mortality in captive elephant populations (Taylor and Poole 1998; Dale 2010). While the majority of publications on zoo elephants focus on acyclicity and potential causes (Yamamoto et al. 2010, Glaeser et al. 2012, Brown et al. 2016), no treatment of the relevance of seasonal reproduction or photoperiodic cueing in elephants exists, to our knowledge (Brown 2014).

We reviewed the literature on the seasonality of reproduction in free-ranging Asian and African elephants and evaluated data on seasonality in captive populations, assessing potential photoperiodic cueing. Additionally, we reviewed literature on other factors affecting reproduction in free-ranging and captive populations, including environmental conditions, social intraspecific interactions and human management.

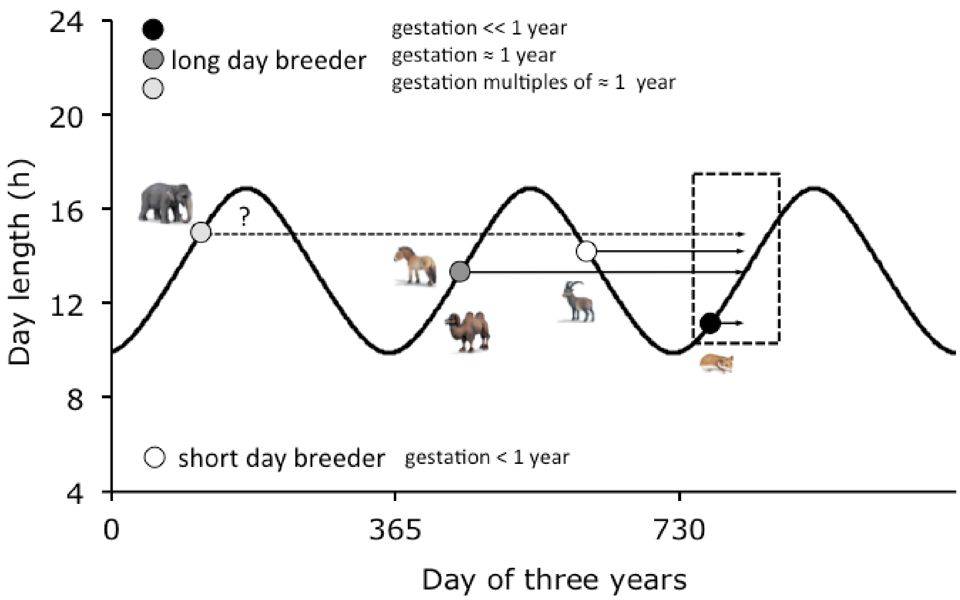


Figure 1 Schematic concept of the interrelation between photoperiodic cueing (direction of day-length change), gestation length (arrows) and the onset of the breeding season (large black, grey and white dots). Assuming a targeted birthing season in spring (when days are getting longer, dashed rectangle), seasonal breeders with very short gestation lengths such as hamsters *Cricetus* spp. are long-day breeders with parturition in the same season (Pévet 1988), seasonal ruminants are short-day breeders with rutting in autumn and gestation lengths of less than one year (Zerbe et al. 2012), and horses (Heck et al. 2017) and camelids (Chen et al. 1985) are long-day breeders with gestation lengths of around one year. Assuming an adaptation to seasonality in elephants, they would be expected to be long-day breeders based on their long gestation length.

METHODS

We searched for literature on reproductive patterns, photoperiodic cueing, seasonal variation in body condition and other factors, using PubMed and Google Scholar to detect relevant literature, as well as both literature cited in and literature citing the publications thus found. For reproductive patterns in free-ranging Asian and African elephant populations, we collected information on seasonal distribution of births or conceptions, on latitude of origin and on timing of dry and wet season from available publications and books. If there was only information on birth patterns, we calculated the respective times of conceptions, taking the Julian start day of the month mentioned as the beginning of the birth season and subtracting the gestation length, using mean lengths of 657 days for Asian elephants and 641 days for African elephants (Lüders 2018), corresponding to approximately 23 months; evaluations based on minimum and maximum reported gestation lengths (Asian elephant: 617 and 693 days; African elephant: 624 and 667 days) are given in Appendix S1. Our approach may yield results that differ from those in studies that assume mean gestation lengths of 20 months or 600 days (e.g. Joshi et al. 2009). The latitude of origin was either given in the publication or was retrieved with Google Latitude Finder (http://www.latlong.net/) by inserting the location of each study. Information about timing of the wet and dry season was either obtained from the same source, or from other publications relating to the same area. Published data were read from graphs using WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/).

To assess whether elephants rely on photoperiodic cueing, we used the Julian start day of breeding and the latitude to calculate the day-length at the onset of the breeding season for those populations for which a seasonal reproductive pattern was reported, using the model developed by Forsythe et al. (1995), and noted whether days were getting longer or shorter at that time. If the conception peak(s) were reported to start in June or December (summer and winter solstices), we allocated peaks in June to the short-day or long-day period, and peaks in December to the long-day or short-day period in the northern or southern hemisphere, respectively. If there were two peaks at different times of the year, we selected the first peak of the year as the beginning of the breeding season. To compare the day-length at the onset of breeding activity between free-ranging and captive populations, we calculated the average day-length for all free-ranging populations. Because photoperiodic signals are not very distinct close to the equator below a latitude of 11.75°N or S (Bronson & Heideman 1994), we also report whether a population reproduces in the short-day or long-day period above this threshold (i.e., further north than 11.75°N or further south than 11.75°S).

To assess captive elephants, we analysed data on births of elephants from Species360 (www.Species360.org), an international non-profit organisation that maintains a database of wild animals held in captivity. We used the method of the Birth Peak Breadth (BPB80), originally developed to quantify the seasonality of reproduction in ruminants (Zerbe et al. 2012), to describe the degree of seasonality as the number of days in which 80% of all births occur. For the calculation of the day-length during the main breeding season, we used the first Julian day of the BPB80 and subtracted the gestation length. For zoo elephants, we set a latitude of 48°N as latitude of origin, as most Asian and African elephants are held in zoos at latitudes from 43 to 53°N.

BREEDING SEASONALITY IN ASIAN ELEPHANTS

Free-ranging elephants

Free-ranging Asian elephants are capable of breeding throughout the year, but 7 of 10 studies reviewed reported seasonal distribution or seasonal conception peaks (Table 1). Generally, available data on the timing of conceptions or births in free-ranging Asian elephants are scarce.

Two early studies stated that in Sri Lanka, near the equator, the distribution of births and conceptions does not follow a seasonal pattern, although there may not have been enough data to exclude seasonality in reproduction, as numbers of observed matings, births and populations studied were not indicated (Phillips 1935, McKay 1973). Another early study reported conceptions to peak at the beginning of the wet season in the short-day period in Sri Lanka (Eisenberg & Lockhart 1972). Other researchers found that the peak of conceptions in Sri Lanka coincided either with the dry season in the short-day period (Santiapillai et al. 1984) or the long-day period (De Silva et al. 2013), with the wet season in the short-day period (Ishwaran 1981), or with the wet season in the long-day period (Kurt 1974, Katugaha et al. 1999; Table 1).

In India, at higher latitudes, Joshi et al. (2009) found conceptions to increase in the dry season in the long-day period, whereas Ramesh et al. (2011) did not identify any seasonal distribution of births in a population living in a rather aseasonal environment (Table 1).

The day-length at the onset of breeding activity or peak reproductive activity varied from 10.7 to 12.5 hours (average 11.9 hours) at latitudes from 6.29°N to 30.13°N (Table 2). In 4 of 7 reviewed studies reporting a seasonal pattern for free-ranging Asian elephants, the breeding season started in the long-day period (Table 3). Counting only populations that lived at latitudes higher than 11.75°N, one free-ranging population did not show any seasonal breeding pattern

(Ramesh et al. 2011) in an aseasonal environment, and the other started breeding in the long-day period which coincided with the dry season (Joshi et al. 2009; Table 1).

Table 1 Distribution of conceptions and conception peaks (estimated with the mean gestation length) in free-ranging and semi-captive Asian elephants *Elephas maximus* in relation to the rainy season, the long-day or short-day period and the working season in the timber industry

Latitude	Month												n	Source
	J	F	M	A	M	J	J	A	S	O	N	D		
	days getting longer						days getting shorter							
6.29°N					xx	xx	xx	xx					84	a
6.64°N						x	x	x	x				3	b
6.64°N	xx	xx	xx	xx	xx	xx							325	c
6.64°N		x	x		x								3	*d*
7.28°N										xx	xx		41	e
7.87°N	-	-	-	-	-	-	-	-	-	-	-	-	-	*f*
7.87°N									xx				-	*g*
7.87°N	-	-	-	-	-	-	-	-	-	-	-	-	-	*h*
10.42°N	xx	xx	xx										261	*i
11.38°N	-	-	-	-	-	-	-	-	-	-	-	-	1 pop.	j
18.79°N	xx	xx	xx	xx	xx							xx	22	+k
21.91°N	xx	xx	xx	xx									3070	*l
21.91°N	xx	xx	xx	xx									2350	*m
26.62°N	xx	xx	xx	xx	xx								51	+n
30.13°N		xx	xx	xx	xx	xx							1 pop.	o

x= most conceptions take place; xx= conception peaks or increased number of females in oestrus; - = conceptions evenly distributed; light grey squares = rainy season; dark grey squares = resting time (Feb-May; Mar 2002); n= number of observed births/matings/studied populations (- = number not indicated); Sources: *from timber working camps, + semi-captive, *italic=data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Phillips 1935*, *g Eisenberg & Lockhart 1972, h McKay 1973*, i Sukumar et al. 1997, j Ramesh et al. 2011, k Thitaram et al. 2008, l Mar 2002, m Mumby et al. 2013, n Baskaran et al. 2009, o Joshi et al. 2009.

Semi-captive elephants

Semi-captive Asian elephants conceive all year round, but in all studies we reviewed a seasonal pattern of reproduction was reported (Table1). In Thailand, at 18.79°N, Thitaram et al. (2008) reported a seasonal reproductive pattern in semi-captive elephants used for tourist riding; the peak of female oestrus was at the beginning of the long-day period during the dry season (Table 1). Dry season is the peak tourist season in Thailand (December to March).

In India, at 10.42°N, Sukumar et al. (1997) reported conceptions to occur mainly in the long-day period in the dry season in two timber camps (Fig. 2) and Baskaran et al. (2009), who studied semi-captive Asian elephants used in tourism and for patrolling in the forests, also observed seasonal breeding in the long-day period in the dry season (Table 1).

In Myanmar, at 21.91°N, Asian elephants used for work in the timber industry also showed a seasonal pattern of reproduction (Table 1). Most conceptions occurred in the long-day period during the dry season (Mar 2002, Mumby et al. 2013). The conception peak was in February, which was the end of the working season, and the breeding period lasted until shortly before the resumption of work in June (Table 1).

Table 2 Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the mean gestation length in free-ranging and semi-captive Asian elephants *Elephas maximus* at different latitudes

Latitude	Julian start day	Day-length [hours/day]	Timing	Source
6.29°N	121	12.3	L	a
6.64°N	152	12.5	S	b
6.64°N	1	11.7	L	c
6.64°N	32	11.8	L	*d*
7.28°N	274	12.1	S	e
7.87°N	244	12.3	S	*f*
10.42°N	1	11.5	L	*g
18.79°N	335	11.1	**L**	+h
21.91°N	1	10.8	**L**	*i
21.91°N	1	10.8	**L**	*j
26.62°N	1	10.5	**L**	+k
30.13°N	32	10.7	**L**	l

Sources: *from timber working camps, + semi-captive, *italic= data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Eisenberg & Lockhart 1972*, g Sukumar et al. 1997, h Thitaram et al. 2008, i Mar 2002, j Mumby et al. 2013, k Baskaran et al. 2009, l Joshi et al. 2009.

The day-length at the onset of breeding season or peak mating activity varied from 10.5 to 11.5 hours per day (average 10.9 hours) at latitudes from 10.42°N to 26.62°N (Table 2). In all of the reviewed studies breeding season or conception peaks started in the long-day period and coincided with the dry season. With the exception of the population studied by Sukumar et al. (1997), all these populations lived at latitudes further north than 11.75°N.

Calculating the main breeding activity with the minimum gestation length had no relevant effect on the results; using the maximum gestation length, however, reduced the number of studies that indicated long-day breeding (Table 3), because breeding activity changed close to the equinox (Table 1).

Table 3 Number of studies (of all studies; number in parentheses) suggesting short-day or long-day breeding activity after the calculation of the breeding season with the minimum, mean or maximum gestation length (for the total of studies / those from latitudes further north than 11.75°N), with indication of the number of changes from short-day to long-day (S-L) or long-day to short-day (L-S) breeding, compared to the mean gestation length in free-ranging and semi-captive Asian elephants *Elephas maximus*. Sources in Table 1

Gestation length	Minimum (617 days)	Mean (657 days)	Maximum (693 days)
Short-day breeding (total/above 11.75°N)	4(12)/0(5)	3(12)/0(5)	8(12)/3(5)
Long-day breeding (total/above 11.75°N)	8(12)/5(5)	9(12)/5(5)	4(12)/2(5)
Change S-L/L-S	0/1	-	0/5

Captive elephants
In Sri Lanka at a latitude of 6.88°N, captive Asian elephants at the Pinnawala Elephant Orphanage showed conception peaks in the wettest months from September to October in the short-day period (Pushpakumara et al. 2016).

For Asian elephants housed in zoos all over the world, the BPB80 was quite long, at 276 days, indicating aseasonal reproduction. A steady increase in conceptions was recorded from January on, with a peak in May or June; conception rates were stable throughout autumn and the lowest number of conceptions occurred in October and November. Focused on zoos at latitudes from 43 to 53°N (average 48°N), where the largest numbers of Asian elephants are held in captivity, again, more conceptions were recorded from February on, conceptions peaked both in June and again in the beginning of September, and consequently reproductive activity was low from October to January (Fig. 2). Using the first day of BPB80 as the start of the birth season, captive Asian elephants held at latitudes from 43 to 53°N (average 48°N) increased breeding activity from Julian day 73 in the long-day period onward, on average when day-length was 11.7 hours. Compared to the average of free-ranging populations, they increase breeding activity earlier in the year.

BREEDING SEASONALITY IN AFRICAN ELEPHANTS

Free-ranging elephants
Like Asian elephants, free-ranging African elephants are capable of breeding year-round, but 21 of 24 studies reviewed reported seasonal reproduction or conception peaks (Table 4). Depending on the location in Africa, there are two rainy seasons (usually from March to May and from October to December) interrupted by a shorter and a longer dry season close to the equator, or one long rainy season (usually from November to April) at higher latitudes.

All studies from habitats with two rainy seasons, at low latitudes, revealed a seasonal pattern of reproduction. In one of the 10 studies, the breeding season was reported to start prior to the rainy season(s) in the long-day period (Laws 1970; Table 4). Although conception peaks varied from year to year in the study conducted by Poole (1987), the peaks started on average just at the onset of each rainy season, with the first peak of the year occurring in the long-day period. Laws et al. (1975) reported three conception peaks throughout the year, taking place just at the onset of the rainy season in the short-day period and during the dry season as well as at the end of the second rainy season in the long-day period. In 7 of 10 studies from habitats with two rainy seasons, conceptions mainly occurred towards the end of the rainy season or at the beginning of the dry season, and in 5 of 7 studies they mainly occurred in the short-day period (Table 4).

Table 4 Distribution of conceptions and conception peaks (estimated with the mean gestation length) by month in free-ranging African elephants *Loxodonta africana* in relation to the rainy season and the long-day or short-day period

Latitude	Month												n	Source
	J	F	M	A	M	J	J	A	S	O	N	D		
	days getting longer						days getting shorter							
2.15°N							xx	xx	xx	xx	xx		24	*a*
2.15°N	xx										xx	xx	282	*b*
1.37°N		x	x						x	x			5 pop.	c
1.37°N	xx	xx	xx									xx	31	*d*
0.61°N	x			x	x	x					x	x	203	e
0.61°N	xx			xx	xx	xx						xx	111	f
	days getting shorter						days getting longer							
0.60°S			xx					xx				xx	-	g
2.65°S	x	x	x	x	x	x						x	1030	h
2.65°S		x	x	x	x	x	x	x	x				1360	i
2.65°S	xx		xx	xx	xx	xx					xx	xx	-	j
4.00°S	x	x	x	x	x	x							82	k
4.31°S	xx	xx	xx	xx	xx	xx					xx	xx	85	*l*
9.00°S										x	x		-	m
11.91°S	x	x	x	x							x	x	179	n
13.13°S	x	x	x	x	x							x	-	o
18.45°S	x	x	x	x							x	x	64	p
19.02°S	-	-	-	-	-	-	-	-	-	-	-	-	-	q
22.33°S	-	-	-	-	-	-	-	-	-	-	-	-	-	r
23.99°S	xx	xx	xx								xx	xx	59	s
23.99°S	-	-	-	-	-	-	-	-	-	-	-	-	-	t
23.99°S	x	x	x	x							x	x	353	u
23.99°S	xx	xx								xx	xx	xx	695	v
30.56°S	x	x	x								x	x	-	w
33.48°S		xx	xx								xx		109	x

x = over 70% of the conceptions take place; xx = conception peaks or increased number of females in oestrus; - = conceptions evenly distributed; grey squares = rainy season; n= number of observed births/matings/studied populations (- = number not indicated); Sources: *italic= data limited; a Buss & Smith 1966, b Buechner et al. 1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972,* m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Ansell 1960, r Smithers 1971, s Hall-Martin 1987, t Fairall 1968, u Smuts 1975, v Freeman et al. 2009b, w Craig 1984, x Hall-Martin 1987.

Moss et al. (2011) found an association between rainfall and conceptions, with peak conceptions occurring two months after peak rainfall.

In habitats with only one rainy season, at higher latitudes, three studies observed an aseasonal pattern of reproduction, although the numbers of observed births, matings or populations studied were not reported (Ansell 1960, Fairall 1968, Smithers 1971). However, most (and more recent) studies reported seasonal breeding. In only one study did conceptions begin to peak before the onset of the single rainy season in the long-day period, and that peak only lasted about two months (Verheyen 1951). In 9 of 14 habitats with a single rainy season, conceptions peaked or took place from the onset of the rainy season or shortly after its onset, and in 7 of the 9 studies conceptions peaked in the long-day period (Table 4). Freeman et al. (2009b) showed that the mean percentage of conceptions for each month was positively correlated with the mean monthly precipitation. Hall-Martin (1987) observed two conception peaks throughout the year in a population in South Africa, one just after the onset of the rainy season in the long-day period, and another towards its end in the short-day period (Table 4).

Table 5 Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the mean gestation length in free-ranging African elephants *Loxodonta africana* at different latitudes

Latitude	Julian start day	Day-length [hours/day]	Timing	Source
2.15°N	182	12.2	S	*a*
2.15°N	305	12.0	S	*b*
1.37°N	32	12.1	L	c
1.37°N	335	12.0	L	*d*
0.61°N	305	12.1	S	e
0.61°N	335	12.1	L	f
0.60°S	60	12.1	S	g
2.65°S	335	12.3	S	h
2.65°S	32	12.2	S	i
2.65°S	305	12.2	L	j
4.00°S	1	12.3	S	k
4.31°S	305	12.3	L	l
9.00°S	274	12.2	L	m
11.91°S	305	12.5	**L**	n
13.13°S	335	12.8	**S**	o
18.45°S	305	12.8	**L**	p
23.99°S	305	12.9	**L**	q
23.99°S	305	12.9	**L**	r
23.99°S	274	12.3	**L**	s
30.56°S	305	13.3	**L**	t
33.48°S	32	13.7	**S**	q

Sources: *italic= data limited; a Buss & Smith 1966*, *b Buechner et al. 1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972*, m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Hall-Martin 1987, r Fairall 1968, s Smuts 1975, t Craig 1984

In addition to the results above, some authors not only reported fluctuations of conceptions throughout one year, but also low conception rates in years with less rain and many conceptions in years with a lot of rain in populations living near the equator (Douglas-Hamilton 1972, Moss 2001, Sukumar 2003, Moss et al. 2011).

The day-length at the onset of mating activity or peak breeding season varied from 12.0 to 13.7 hours per day (average 12.4 hours) at latitudes from 33.48°S to 2.15°N. In 12 of 21 reviewed studies reporting a seasonal pattern, breeding season or conception peaks started in the long-day period. Counting only populations further south than 11.75°S and reproducing seasonally, 6 of 8 had conception peaks that started in the long-day period and at the beginning of the wet season (Table 5).

Calculating the main breeding activity with the minimum and maximum gestation length both increased the number of studies that indicated long-day breeding (Table 6), because breeding activity started to increase around the middle of the long-day period (Table 3).

Table 6 Number of studies (of all studies; number in parentheses) suggesting short-day or long-day breeding activity after the calculation of the breeding season with the minimum, mean or maximum gestation length (for the total of studies / those from latitudes further south than 11.75°S), with indication of the number of changes from short-day to long-day (S-L) or long-day to short-day (L-S) breeding compared to the mean gestation length in free-ranging African elephants *Loxodonta africana*. Sources in Table 4

Gestation length	Minimum (624 days)	Mean (641 days)	Maximum (667 days)
Short-day breeding (total/beyond 11.75°S)	8(21)/2(8)	9(21)/2(8)	7(21)/1(8)
Long-day breeding (total/beyond 11.75°S)	13(21)/6(8)	12(21)/6(8)	14(21)/7(8)
Change S-L/L-S	2/1	-	2/0

Captive elephants

Apart from the data from zoo elephants below, there were few reports on seasonality of reproduction in African elephants held in zoos, but ovarian inactivity in African zoo elephants more often occurred between December and early April (Schulte et al. 2000).

For captive African elephants housed in zoos all over the world, the BPB80 was again long, at 255 days, also indicating aseasonal reproduction. An increase of conceptions was recorded from the beginning of the year on with a major peak in June, followed by a low number of conceptions for the rest of the year. Considering only the elephants at latitudes from 43 to 53°N (average 48°N), again, more conceptions were recorded from February on, with a peak in May or June and a lower number of conceptions at other times of the year (Fig. 2). Captive African elephants held at latitudes from 43 to 53°N (average 48°N) increased their breeding activity from Julian day 95 onwards in the long-day period, starting on average when day-length was 13.0 hours. Compared to the average of free-ranging populations, they increased their breeding activity earlier in the year.

FACTORS INFLUENCING REPRODUCTION IN FREE-RANGING, SEMI-CAPTIVE AND CAPTIVE ELEPHANT POPULATIONS

Photoperiod

Mammals in temperate zones usually reproduce seasonally and rely on photoperiodic cueing (Bronson & Heideman 1994). The underlying physiological mechanism is the synthesis and secretion of melatonin by the pineal gland, which peak during the night. The longer the night, the more melatonin is produced; melatonin inhibits or stimulates the reproductive axis of long-day and short-day breeders, respectively (viviD & Bentley 2018). Latitude is important for photoperiodicity; changes in day-length are more pronounced at higher latitudes. Below 30°N or S, photoperiodicity becomes gradually less useful until its value is lost in the mid to deep tropics (below 11.75°N or S; Bronson & Heideman 1994). The elephants' ancestors originated from the African continent, where they evolved in a tropical climate at latitudes near the equator (Van der Made 2010). Only when ancient proboscideans had evolved a tooth structure adapted to grasses (Cerling et al. 1999) was it possible for them to disperse out of Africa into South Asia and into more seasonal regions (Van der Made & Mazo 2003, Van der Made 2010) where the evolution of a seasonal reproduction cued by photoperiodicity would have been advantageous. The absence of a common day-length linked to breeding activity (Tables 2 and 5) indicates that it is likely to be the day-length change *per se*, rather than the absolute day-length, that triggers breeding. Free-ranging Asian elephants living at higher latitudes, as well as semi-captive and captive Asian elephant populations reviewed in our study, show a moderate preference for long-day breeding (Tables 1-3). The studies reporting breeding to start in the short-day period were conducted either on populations living close to the equator or with very limited data (Eisenberg & Lockhart 1972, Ishwaran 1981, Santiapillai et al. 1984). The reviewed population of free-ranging Asian elephants living in the highest latitude increased breeding in the long-day period and in the dry season (Joshi et al. 2009), providing strong support for a photoperiodic control in elephant reproduction. Free-ranging African elephants living at lower latitudes did not show a preference for long-day or short-day breeding either, whereas most of the populations living at higher latitudes increased breeding in the long-day period (Tables 4-6). Again, studies reporting the breeding season to start in the short-day period were mostly conducted on populations living close to the equator or with limited data (Buechner et al. 1963, Buss & Smith 1966, Laws et al. 1975, Foley et al. 2001, Wittemyer 2001), or on a population without a highly seasonal breeding pattern (Moss 2001, Moss et al. 2011).

Several authors reported the occurrence of oestrus synchrony in free-ranging Asian and African elephant populations (Hanks 1972, Santiapillai et al. 1984, Sukumar 2003), and Weissenböck et al. (2009) provided the first evidence for oestrus synchrony in captive African elephants. Oestrus synchrony could be the result of a photoperiodic cue or good environmental conditions, leading to initiation of oestrus in many females at once. Other reasons for the synchronisation of oestrus in elephants could be as an antipredator strategy in order to provide protection through group defence of the calves following their mothers at heel (Santiapillai et al. 1984) or to allow the benefits of allomothering exhibited in elephant herds (Rasmussen and Schulte 1998, Moss et al. 2011).

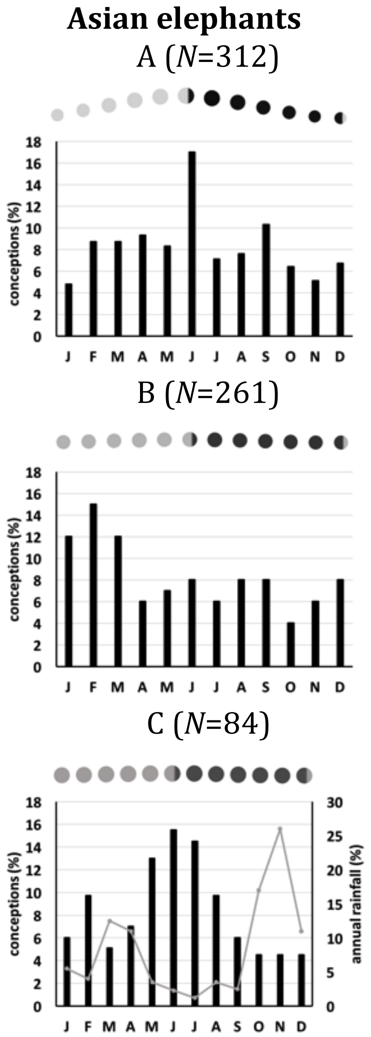
Reliance on photoperiodic cueing could also explain why captive elephants showed rather low reproductive activity throughout winter, despite their generally high body condition. A high body condition does not necessarily mean an ideal one, as a score of 4 or 5, which is common amongst captive elephants, indicates overweight or even obesity (Morfeld et al. 2016). The captive populations increased breeding earlier in the year than their wild conspecifics. In domesticated farm animals such as sheep and goats (short-day breeders), simulating short days through artificial light was reported to reset the onset of reproductive activity (Chemineau et al. 2008). In horses (long-day breeders), exposure to long days through artificial light during winter also led to ovulations 2-3 months earlier than usual (Guillaume 1996). Because many captive elephants are primarily housed inside during the winter months, the influence of lengthened days due to artificial lighting could have caused a reset of reproductive activity; alternatively, the more distinct differences in day-length at higher latitudes could provide a stronger signal with an earlier effect.

Nutrition and body condition

Whereas Laws and Parker (1968) argued that giving birth before peak rainfall, timed by photoperiod, ensures an optimal body condition for lactating elephant cows, Ogutu et al. (2015) suggested that the food quality around the time of oestrus and mating rather than at the time of parturition is the factor which controls reproductive patterns in elephants. Supporting this, conceptions rather than births were found to be linked to local rainfall patterns by Freeman et al. (2009b). Generally, it is very difficult to disentangle the factors photoperiod and body condition from one another (Fig. 2).

The body condition of free-ranging Asian elephants in India changed significantly between the seasons, as well as the faecal glucocorticoid levels which were strongly negatively associated with the body condition score (Pokharel et al. 2017). Mumby et al. (2015b) reported the same pattern for semi-captive Asian elephants in timber camps in Myanmar: the highest overall body weight was measured during monsoon months and the lowest towards the end of the dry season. By contrast, a recent study on Sri Lankan elephants found that their body condition was better in the dry season, probably because the receding water levels in reservoirs offered space for fresh grass regrowth (Ranjeewa et al. 2018). As described above, free-ranging Asian elephants at higher latitudes and semi-captive Asian elephants showed a moderate preference for long-day breeding, even though the long-day period more often coincided with the dry season when body condition was lower. The captive population of the Pinnawala Elephant Orphanage in Sri Lanka is one of the few Asian elephant populations with a preference for short-day breeding. However, these elephants live near the equator and are fed a sufficient amount of food, so matings are enabled throughout the year (Pushpakumara et al. 2016). As the quality of forage in that area was highest at the time when conceptions peak (Pushpakumara et al. 2016), it is likely that nutrition and body condition had an influence on the conception peak in this population.

The body condition of free-ranging African elephants is significantly lower during the dry season than during the wet season (Laws & Parker 1968, Foley et al. 2001). At higher latitudes, free-ranging African elephants showed a preference for long-day breeding and, although the wet season usually started in the long-day period, often together with the breeding season, many more wet months fell in the short-day period and body condition improved during the course of the rainy season (Foley et al. 2001).



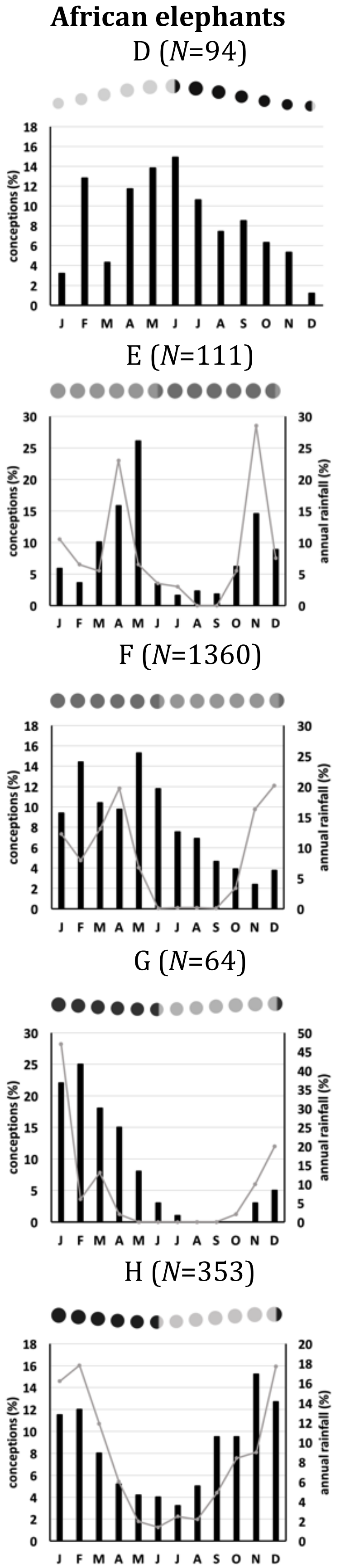


Figure 2 Monthly proportion of conceptions and rainfall (if data were available) over the year in Asian and African elephants in zoos from latitudes 43 to 53°N and in different natural habitats; short-day (dark) and long-day (light) periods are indicated by sun symbols and the extent of day-length variation over the year in the different latitudes is indicated by the different amplitudes and colour graduations of these symbols (the greater the day length difference the greater the contrast between dark and light), calculated with the mean gestation length: A) captive Asian elephants in zoos from latitudes 43 to 53°N; B) free-ranging Asian elephants, Mudumalai National Park (10.42°N), India, Sukumar et al. (1997); C) free-ranging Asian elephants, Udawalawe National Park (6.29°N), Sri Lanka, De Silva et al. (2013); D) captive African elephants in zoos from latitudes 43 to 53°N; E) free-ranging African elephants, Samburu National Reserves (0.61°N), Kenya, Rasmussen (2001); F) free-ranging African elephants, Amboseli National Park (2.65°S), Kenya, Moss (2011); G) free-ranging African elephants, Wankie National Park (18.45°S), Zimbabwe, Williamson (1976); H) free-ranging African elephants, Kruger National Park (23.99°S), South Africa, Smuts (1975)

For captive populations, seasonal dietary changes are not reported, and it can be assumed that they are provided with a sufficient amount of food year-round (Freeman et al. 2004). Data available from captive elephant populations in Europe indicates that there is no seasonal variation of body condition in captivity (Schiffmann, pers. obs.), and obesity, rather than poor body condition, is a problem (Freeman et al. 2004, Morfeld et al. 2016). Whereas obesity in captive Asian females is not associated with acyclicity, it was found to be associated with reproductive problems in captive African elephants (Freeman et al. 2009a), although current research in zoos revealed no correlation between fat mass and cyclic reproductive activity in female African elephants (Chusyd et al. 2018). If mainly nutrition and body condition affected reproduction in elephants, we would expect captive elephants to breed completely aseasonally, due to their constantly high body condition. The fact that captive elephants start increasing their breeding activity earlier than their free-ranging conspecifics may also be an effect of their higher body condition. Seasonal ruminant species for example, relying on photoperiod and maintaining a seasonal pattern in captivity, start breeding earlier in the year than they would in the wild if they were in better body condition (Montgomery et al. 1985).

Intraspecific interactions

Social interactions were suspected to influence reproductive patterns in free-ranging African elephants, especially in big groups and among lower-ranked elephants (Douglas-Hamilton 1972, Dublin 1983, Rasmussen & Schulte 1998, Foley et al. 2001), whereas no observations are available for free-ranging Asian elephants. Dublin (1983) found calves of dominant African elephant cows to be born earlier in the rainy season than those of subordinate females. However, Freeman et al. (2009b) did not find an association between conception month or birth month and age of the female, though age is related to social status in elephants, and Moss et al. (2011) found no evidence of reproductive suppression in animals of subordinate status either. Elephants show oestrus synchrony (Hanks 1972, Santiapillai et al. 1984, Sukumar 2003) and highly co-operative rearing behaviour. This results in larger families being more reproductively successful due to a greater number of allomothers, protectors and older, more experienced matriarchs (Moss et al. 2011).

In captive Asian elephants, dominance rank was not reported to influence ovarian activity, whereas hierarchy was suspected to influence the reproductive state of captive African females (Glaeser et al. 2012), where ovarian inactivity was associated with a high social dominance rank (Freeman et al. 2004). Schulte et al. (2000), on the other hand, measured the longest duration of temporary ovarian inactivity or acyclicity in the most subordinate female in a captive African elephant population.

Several authors found acyclicity to be related to hyperprolactinemia (Yamamoto et al. 2010, Brown et al. 2016) and levels of prolactin were found to be positively correlated with cortisol levels in captive African elephants (Bechert et al. 1999), with high levels probably indicating social stress (Brown et al. 2016). Whereas free-ranging African elephants live in family units consisting of mainly related females and their offspring, female elephants in zoos are often unrelated (Freeman et al. 2004, Moss et al. 2011). Unrelated free-ranging female African elephants that were disrupted from their families had higher faecal glucocorticoid concentrations and a lower reproductive output than females in groups of relatives (Gobush et al. 2008). Additionally, captive Asian and African elephants show reduced reproductive activity in winter, suggesting that higher social stress due to closer proximity to unrelated females whilst mainly being housed inside during winter may influence reproduction (Schulte et al. 2000).

Another factor possibly influencing seasonal reproduction in elephants is the phenomenon of musth in males. Males in musth are more likely to breed, and were observed searching actively for females in oestrus (Poole 1989, Moss et al. 2011). In free-ranging African elephants in the Amboseli National Park, DNA analysis revealed that 74% of sires were in musth at the time of conception (Hollister-Smith et al. 2007). In a study on captive Asian elephants in the USA, no correlation between the onset of musth and the onset of oestrus was found (Duer et al. 2016), but Dow et al. (2011) measured slightly higher cyclicity rates (by approximately 11%) in female African elephants in facilities housing a bull than in those without a bull.

It is possible that contact with females in oestrus initiates the state of musth in male elephants (Poole 1989, Lincoln & Ratnasooriya 1996), or the other way around. The peak of males in musth started shortly before the peak of females in oestrus in most of the reviewed free-ranging Asian elephant populations, and a high proportion of male African elephants were in musth just at the time when many females were noted to be in oestrus (Poole 1989, Lincoln & Ratnasooriya 1996, Katugaha et al. 1999, Thitaram et al. 2008, Joshi et al. 2009, Moss et al. 2011). Musth and oestrus may occur at the same time due to favourable conditions for both, or due to a photoperiodic effect. There are very few data on the timing of musth and its influence on females in captivity; it would be interesting to investigate photoperiodic cueing in males in the future (Dow et al. 2011, Duer et al. 2016).

Other environmental stressors

In Asian elephants, heat stress was suspected to lead to delayed ovulation (Thitaram et al. 2008). Mumby et al. (2015b) measured the highest cortisol metabolite levels in semi-captive Asian timber elephants in Myanmar not during the dry season, but in the first three months of the monsoon season (June to October; Fig. 3). It is still hot at that time and the month of June also coincides with the restart of the working season after a break from February to May (Mar 2002). In many regions in Africa, temperatures reach their maximum during the rainy season, especially in January and February, and are lowest from June to October (Moss 2001, Freeman et al. 2009b, Moss et al. 2011), whereas overall cortisol metabolite concentrations were found to be highest during the dry season (Foley et al. 2001). Slightly elevated cortisol concentrations were measured in the coldest (January) and hottest (August) months in captive African elephants in a zoo in Indianapolis, USA (Brown et al. 2010).

Any kind of stress, such as high or low temperatures, high humidity or heavy workload, is likely to affect reproduction. Despite the heat and humidity, conceptions still occur or even peak in Asian elephants at the time when temperatures are highest in South Asia (Table 1). In the semi-captive working elephants, the sudden onset of intense physical workload might also explain the elevated glucocorticoid levels at the beginning of the monsoon, which could potentially cause long-term cessation of oestrus cycles in elephants (Mumby et al. 2015b). The contributions of timber work and climate to cortisol levels cannot be disentangled based on those data. However, conceptions already started to peak shortly before the work break in the long-day period in Myanmar, and in working elephants in Thailand peaks occurred in the long-day period when temperatures were high, body condition low and despite the coincidence with the peak tourist season (Thitaram et al. 2008). This can be viewed as strong support for a photoperiodic control in elephant reproduction.

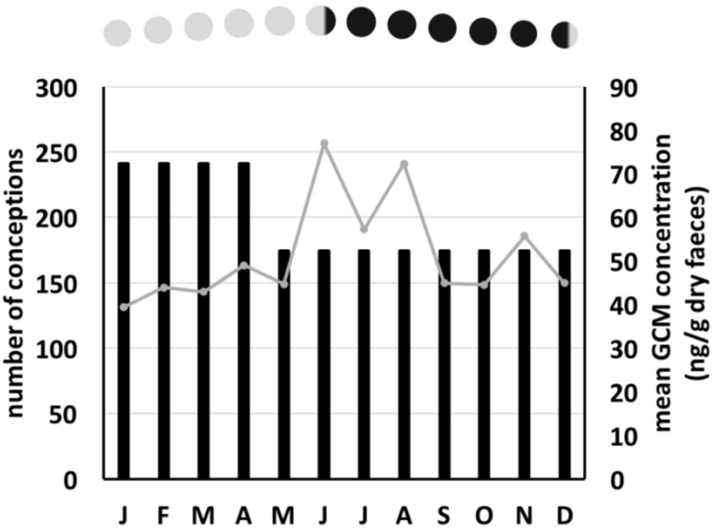


Figure 3 Mean monthly glucocorticoid metabolite concentration (GCM) in faeces of female Asian elephants aged 17-55 years (N=37) from timber work camps in Myanmar (21.91°N; grey line) (Mumby et al. 2015a) and number of conceptions by month of timber elephants in Myanmar calculated with the mean gestation length (black bars; Mumby et al. 2013; 41% of conceptions took place from Feb-May, N= 2350, average conceptions calculated for each month). Feb-May = rest time, Jun = start of working period and monsoon (Mar 2002). For meaning of sun symbols, see Fig. 2.

The reproduction of free-ranging African elephants was not reported to be affected by heat, cold or humidity, and the elevated cortisol metabolite concentrations measured during the dry season in free-ranging African elephants were probably caused by limited access to food and water (Foley et al. 2001). As elephants in zoos are provided with heated shelters in winter and shaded structures in summer, temperature should not have an influence on their reproduction. The reviewed data on captive Asian elephants from latitudes 43 to 53°N show that conceptions were at the lowest level in the coldest month (January) and at a low (but not at the lowest) level in the hottest month (August); conceptions in captive African elephants were at a low level in the coldest month and at a medium level in the hottest month (Fig. 2). If anything, in temperate zones cold, rather than heat, has a negative effect on reproduction, at least in captive African elephants.

Human activities can greatly influence elephant reproduction. In addition to illegal poaching for ivory, management actions such as contraception or translocations have a major impact (Dickson & Adams 2009, Owens & Owens 2009). The life and reproduction of captive elephants is almost fully controlled by human management. Access to suitable bulls is often restricted in zoo populations and the age structure of males is often not ideal for breeding. Female elephants prefer larger, older males and they also prefer males in musth (Sukumar 2003, Moss et al. 2011, Toeffels 2015). Semi-captive female elephants in Thailand are separated from males, but are exposed to them regularly at a distance. Access is provided if increased sexual behaviour is observed (Thitaram et al. 2008). In Myanmar, the timber elephants are able to socialise with camp and free-ranging elephants during the night (Mar 2002) and are held in mixed herds. Of the European institutions belonging to the European Endangered Species Program, only 44% provided their female elephants with access to a male in 2009 (Prahl 2009).

Brown et al. (2016) found that enrichment diversity and percentage of time with access to conspecifics was negatively correlated with reproductive acyclicity in zoo elephants. Enrichment through food is common in captive elephants, and is apparently presented more often during winter (Posta et al. 2013); contact with conspecifics is closer during winter when the elephants are mainly housed inside. Thus, we would expect fewer acyclic elephants at that time, which does not correspond to our findings. The most important factor for successful reproduction in captive elephant populations may be the availability of suitable males that can be given access to healthy, receptive cows at the right time (Prahl 2009, Toeffels 2015). When captive females are in oestrus, keepers usually bring them together with a bull if one is available. However, during winter when elephants are mainly housed inside, space for breeding is usually restricted. Therefore, human management might bias the apparent moderate seasonality of reproduction. The extent of that influence remains to be investigated.

CONCLUSIONS

Although Asian and African elephants are able to reproduce year-round, they show a moderate seasonal pattern of reproduction. The findings can be interpreted as indicative of an underlying photoperiod-triggered system that receives additional input from body condition and stress status. Based on our results, we hypothesise that elephants are long-day breeders. Because the photoperiod favourable for elephant reproduction in the tropics and subtropics often coincides with other seasonal triggers, such as the wet season and high body condition, it is difficult to tease these different factors apart. Elephant habitats are often characterised by rather unpredictable climatic conditions, at least in the mid- to deep tropics (as compared to more predictable temperate-zone habitats); therefore, relying completely on photoperiodicity would not be beneficial. Correspondingly, published data indicate an underlying photoperiodic influence that can be modified and even overruled by other factors.

Captive elephant populations in zoos are mainly dependent on human management. Obesity, the social composition of the herds, and the degree of enrichment diversity influence the reproductive state of individuals, and access to suitable males at the right time determines the reproductive output of females. To provide an environment that preserves and encourages a natural breeding pattern, enough free time should be provided for individuals in semi-captive working populations. For zoo elephants, the achievement of an ideal body condition, removal of possible stressors, provision of convenient enrichment, and access to suitable mates is important. We also suggest that managers of captive populations should make use of the potentially naturally occurring photoperiodic cueing, by manipulating female elephants' body condition so that it increases with increasing day-length, as well as by increasing breeding efforts by allowing contact between females and males, especially at the time of year when day-length is increasing.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Appendix S1. Analyses of peak reproductive activity based on minimum and maximum gestation lengths, to supplement Tables 1-2 and 4-5.

SUPPORTING INFORMATION

Appendix S1.

Table S1 minimum Distribution of conceptions and conception peaks (estimated with the minimum gestation length) in free-ranging and semi-captive Asian elephants *Elephas maximus* in relation to the rainy season, the long-day or short-day period and the working season in the timber industry

Latitude	Month												n	Source
	J	F	M	A	M	J	J	A	S	O	N	D		
	days getting longer						days getting shorter							
6.29°N						xx	xx	xx	xx				84	a
6.64°N						x	x	x	x				3	b
6.64°N		xx	xx	xx	xx	xx	xx						325	c
6.64°N			x	x		x							3	*d*
7.28°N											xx	xx	41	e
7.87°N	-	-	-	-	-	-	-	-	-	-	-	-	-	*f*
7.87°N										xx			-	*g*
7.87°N	-	-	-	-	-	-	-	-	-	-	-	-	-	*h*
10.42°N		xx	xx	xx									261	*i
11.38°N	-	-	-	-	-	-	-	-	-	-	-	-	1 pop.	j
18.79°N	xx	xx	xx	xx	xx							xx	22	+k
21.91°N		xx	xx	xx	xx								3070	*l
21.91°N		xx	xx	xx	xx								2350	*m
26.62°N	xx	xx	xx	xx	xx								51	+n
30.13°N			xx	xx	xx	xx	xx						1 pop.	o

x= most conceptions take place; xx= conception peaks or increased number of females in oestrus; - = conceptions evenly distributed; light grey squares = rainy season; dark grey squares = resting time (Feb-May; Mar 2002); *n*= number of observed births/matings/studied populations (- = number not indicated); Sources: *from timber working camps, + semi-captive, *italic=data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Phillips 1935*, *g Eisenberg & Lockhart 1972, h McKay 1973*, i Sukumar et al. 1997, j Ramesh et al. 2011, k Thitaram et al. 2008, l Mar 2002, m Mumby et al. 2013, n Baskaran et al. 2009, o Joshi et al. 2009.

Table S1 maximum Distribution of conceptions and conception peaks (estimated with the maximum gestation length) in free-ranging and semi-captive Asian elephants *Elephas maximus* in relation to the rainy season, the long-day or short-day period and the working season in the timber industry

Latitude	Month												n	Source
	J	F	M	A	M	J	J	A	S	O	N	D		
	days getting longer						days getting shorter							
6.29°N			xx	xx	xx	xx							84	a
6.64°N						x	x	x	x				3	b
6.64°N	xx	xx	xx	xx							xx	xx	325	c
6.64°N	x		x									x	3	*d*
7.28°N								xx	xx				41	e
7.87°N	-	-	-	-	-	-	-	-	-	-	-	-	-	*f*
7.87°N							xx						-	*g*
7.87°N	-	-	-	-	-	-	-	-	-	-	-	-	-	*h*
10.42°N	xx										xx	xx	261	*i
11.38°N	-	-	-	-	-	-	-	-	-	-	-	-	1 pop.	j
18.79°N	xx	xx	xx	xx	xx							xx	22	+k
21.91°N	xx	xx									xx	xx	3070	*l
21.91°N	xx	xx									xx	xx	2350	*m
26.62°N	xx	xx								xx	xx	xx	51	+n
30.13°N	xx	xx	xx	xx								xx	1 pop.	o

x= most conceptions take place; xx= conception peaks or increased number of females in oestrus; - = conceptions evenly distributed; light grey squares = rainy season; dark grey squares = resting time (Feb-May; Mar 2002); *n*= number of observed births/matings/studied populations (- = number not indicated); Sources: *from timber working camps, + semi-captive, *italic=data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Phillips 1935*, *g Eisenberg & Lockhart 1972, h McKay 1973*, i Sukumar et al. 1997, j Ramesh et al. 2011, k Thitaram et al. 2008, l Mar 2002, m Mumby et al. 2013, n Baskaran et al. 2009, o Joshi et al. 2009.

Table S2 minimum Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the mean gestation length in free-ranging and semi-captive Asian elephants *Elephas maximus* at different latitudes

Latitude	Julian start day	Day-length [hours/day]	Timing	Source
6.29°N	152	12.5	S	a
6.64°N	152	12.5	S	b
6.64°N	32	11.8	L	c
6.64°N	60	11.9	L	d
7.28°N	305	11.9	S	e
7.87°N	274	12.1	S	f
10.42°N	32	11.8	L	*g
18.79°N	335	11.1	L	+h
21.91°N	32	11.2	L	*i
21.91°N	32	11.2	L	*j
26.62°N	1	10.5	L	+k
30.13°N	60	11.5	L	l

Sources: *from timber working camps, + semi-captive, *italic= data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Eisenberg & Lockhart 1972*, g Sukumar et al. 1997, h Thitaram et al. 2008, i Mar 2002, j Mumby et al. 2013, k Baskaran et al. 2009, l Joshi et al. 2009

Table S2 maximum Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the mean gestation length in free-ranging and semi-captive Asian elephants *Elephas maximus* at different latitudes

Latitude	Julian start day	Day-length [hours/day]	Timing	Source
6.29°N	60	11.9	L	a
6.64°N	152	12.5	S	b
6.64°N	305	11.9	S	c
6.64°N	335	11.8	L	*d*
7.28°N	213	12.4	S	e
7.87°N	182	12.6	S	*f*
10.42°N	305	11.8	**S**	*g
18.79°N	335	11.1	**L**	+h
21.91°N	305	11.3	**S**	*i
21.91°N	305	11.3	**S**	*j
26.62°N	274	11.9	**S**	+k
30.13°N	335	10.4	**L**	l

Sources: *from timber working camps, + semi-captive, *italic= data limited;* a De Silva et al. 2013, b Santiapillai et al. 1984, c Katugaha et al. 1999, *d Kurt 1974*, e Ishwaran 1981, *f Eisenberg & Lockhart 1972*, g Sukumar et al. 1997, h Thitaram et al. 2008, i Mar 2002, j Mumby et al. 2013, k Baskaran et al. 2009, l Joshi et al. 2009

Table S4 minimum Distribution of conceptions and conception peaks (estimated with the minimum gestation length) by month in free-ranging African elephants *Loxodonta africana* in relation to the rainy season and the long-day or short-day period

Latitude	Month												n	Source
	J	F	M	A	M	J	J	A	S	O	N	D		
	days getting longer						days getting shorter							
2.15°N							xx	xx	xx	xx	xx		24	*a*
2.15°N	xx	xx										xx	282	*b*
1.37°N		x	x						x	x			5 pop.	c
1.37°N	xx	xx	xx									xx	31	*d*
0.61°N	x	x			x	x	x					x	203	e
0.61°N	xx	xx			xx	xx	xx						111	f
	days getting shorter						days getting longer							
0.60°S	xx			xx					xx				-	g
2.65°S	x	x	x	x	x	x	x						1030	h
2.65°S		x	x	x	x	x	x	x	x				1360	i
2.65°S	xx		xx	xx	xx	xx					xx	xx	-	j
4.00°S		x	x	x	x	x	x						82	k
4.31°S	xx	xx	xx	xx	xx	xx	xx					xx	85	*l*
9.00°S										x	x		-	m
11.91°S	x	x	x	x							x	x	179	n
13.13°S	x	x	x	x	x	x							-	o
18.45°S	x	x	x	x							x	x	64	p
19.02°S	-	-	-	-	-	-	-	-	-	-	-	-	-	q
22.33°S	-	-	-	-	-	-	-	-	-	-	-	-	-	r
23.99°S	xx	xx	xx								xx	xx	59	s
23.99°S	-	-	-	-	-	-	-	-	-	-	-	-	-	t
23.99°S	x	x	x	x							x	x	353	u
23.99°S	xx	xx	xx								xx	xx	695	v
30.56°S	x	x	x								x	x	-	w
33.48°S		xx	xx								xx		109	x

x = over 70% of the conceptions take place; xx = conception peaks or increased number of females in oestrus; - = conceptions evenly distributed; grey squares = rainy season; *n*= number of observed births/matings/studied populations (- = number not indicated); Sources: *italic= data limited; a Buss & Smith 1966, b Buechner et al. 1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972,* m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Ansell 1960, r Smithers 1971, s Hall-Martin 1987, t Fairall 1968, u Smuts 1975, v Freeman et al. 2009b, w Craig 1984, x Hall-Martin 1987.

Table S4 maximum Distribution of conceptions and conception peaks (estimated with the maximum gestation length) by month in free-ranging African elephants *Loxodonta africana* in relation to the rainy season and the long-day or short-day period

Latitude	Month												n	Source
	J	F	M	A	M	J	J	A	S	O	N	D		
	days getting longer						days getting shorter							
2.15°N							xx	xx	xx	xx	xx		24	*a*
2.15°N										xx	xx	xx	282	*b*
1.37°N		x	x						x	x			5 pop.	c
1.37°N	xx	xx	xx									xx	31	*d*
0.61°N			x	x	x					x	x	x	203	e
0.61°N			xx	xx	xx						xx	xx	111	f
	days getting shorter						days getting longer							
0.60°S		xx					xx				xx		-	g
2.65°S	x	x	x	x	x						x	x	1030	h
2.65°S		x	x	x	x	x	x	x	x				1360	i
2.65°S	xx		xx	xx	xx	xx					xx	xx	-	j
4.00°S	x	x	x	x	x							x	82	k
4.31°S	xx	xx	xx	xx	xx					xx	xx	xx	85	*l*
9.00°S										x	x		-	m
11.91°S	x	x	x	x							x	x	179	n
13.13°S	x	x	x	x							x	x	-	o
18.45°S	x	x	x	x							x	x	64	p
19.02°S	-	-	-	-	-	-	-	-	-	-	-	-	-	q
22.33°S	-	-	-	-	-	-	-	-	-	-	-	-	-	r
23.99°S	xx	xx	xx								xx	xx	59	s
23.99°S	-	-	-	-	-	-	-	-	-	-	-	-	-	t
23.99°S	x	x	x	x							x	x	353	u
23.99°S	xx								xx	xx	xx	xx	695	v
30.56°S	x	x	x								x	x	-	w
33.48°S		xx	xx								xx		109	x

x = over 70% of the conceptions take place; xx = conception peaks or increased number of females in oestrus; - = conceptions evenly distributed; grey squares = rainy season; *n*= number of observed births/matings/studied populations (- = number not indicated); Sources: *italic= data limited; a Buss & Smith 1966, b Buechner et al. 1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972,* m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Ansell 1960, r Smithers 1971, s Hall-Martin 1987, t Fairall 1968, u Smuts 1975, v Freeman et al. 2009b, w Craig 1984, x Hall-Martin 1987.

Table S5 minimum Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the minimum gestation length in free-ranging African elephants *Loxodonta africana* at different latitudes

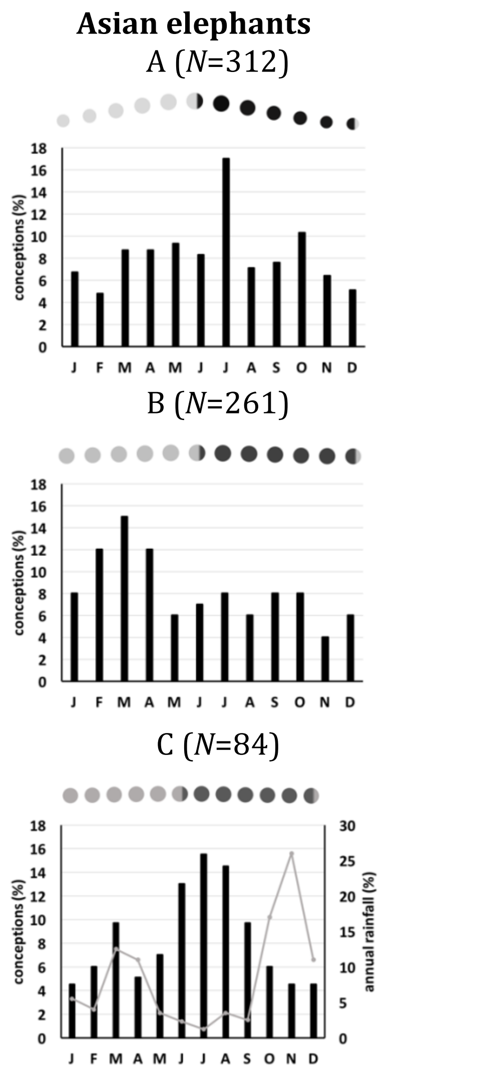
Latitude	Julian start day	Day-length [hours/day]	Timing	Source
2.15°N	182	12.2	S	*a*
2.15°N	335	12.0	L	*b*
1.37°N	32	12.1	L	c
1.37°N	335	12.0	L	*d*
0.61°N	335	12.1	L	e
0.61°N	1	12.1	L	f
0.60°S	1	12.2	S	g
2.65°S	1	12.3	S	h
2.65°S	32	12.2	S	i
2.65°S	305	12.2	L	j
4.00°S	32	12.3	S	k
4.31°S	335	12.3	S	l
9.00°S	274	12.2	L	m
11.91°S	305	12.5	**L**	n
13.13°S	1	12.9	**S**	o
18.45°S	305	12.8	**L**	p
23.99°S	305	12.9	**L**	q
23.99°S	305	12.9	**L**	r
23.99°S	305	12.9	**L**	s
30.56°S	305	13.3	**L**	t
33.48°S	32	13.7	**S**	q

Sources: *italic= data limited; a Buss & Smith 1966*, *b Buechner et al. 1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972*, m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Hall-Martin 1987, r Fairall 1968, s Smuts 1975, t Craig 1984.

Table S5 maximum Day-length at Julian start day of the breeding season including the timing [long-day (L)/short-day period (S)] estimated with the maximum gestation length in free-ranging African elephants *Loxodonta africana* at different latitudes

Latitude	Julian start day	Day length [hours/day]	Timing	Source
2.15°N	182	12.2	S	*a*
2.15°N	274	12.1	S	*b*
1.37°N	32	12.1	L	c
1.37°N	335	12.0	L	*d*
0.61°N	60	12.1	S	e
0.61°N	60	12.1	L	f
0.60°S	32	12.1	S	g
2.65°S	305	12.2	L	h
2.65°S	32	12.2	S	i
2.65°S	305	12.2	L	j
4.00°S	335	12.3	S	k
4.31°S	274	12.1	L	l
9.00°S	274	12.2	L	m
11.91°S	305	12.5	**L**	n
13.13°S	305	12.6	**L**	o
18.45°S	305	12.8	**L**	p
23.99°S	305	12.9	**L**	q
23.99°S	305	12.9	**L**	r
23.99°S	244	11.6	**L**	s
30.56°S	305	13.3	**L**	t
33.48°S	32	13.7	**S**	q

Sources: *italic= data limited; a Buss & Smith 1966*, *b Buechner et al. 1963*, c Laws 1970, *d Perry 1953*, e Wittemyer 2001, f Rasmussen 2001, g Laws et al. 1975, h Moss 2001, i Moss et al. 2011, j Poole 1987, k Foley et al. 2001, *l Douglas-Hamilton 1972*, m Verheyen 1951, n Hanks 1972, o Kerr 1978, p Williamson 1976, q Hall-Martin 1987, r Fairall 1968, s Smuts 1975, t Craig 1984.



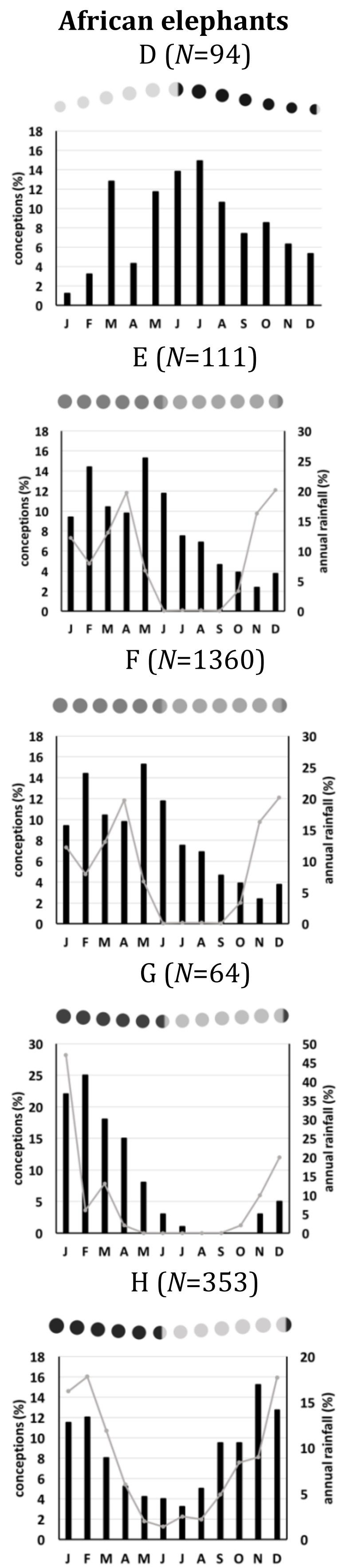
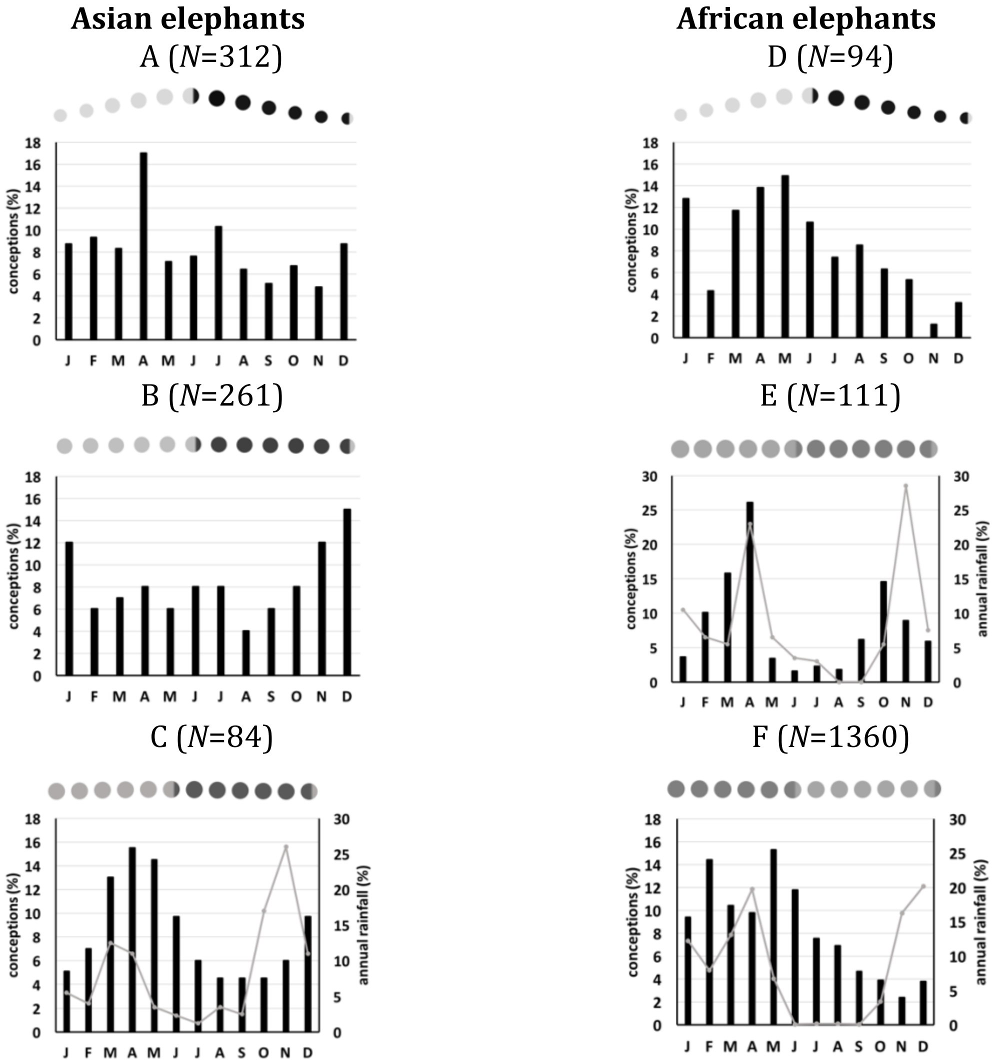
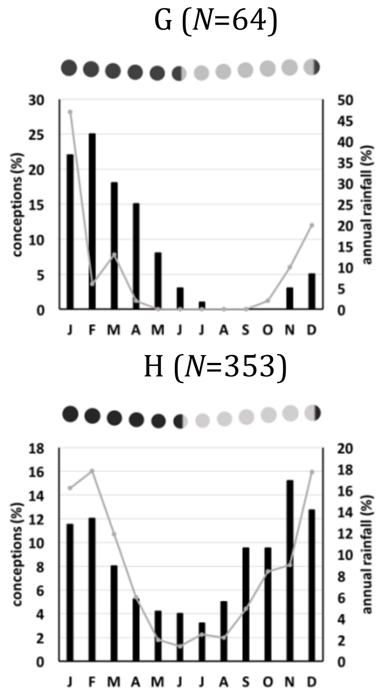


Figure S2 minimum Monthly proportion of conceptions and rainfall (if data were available) over the year in Asian and African elephants in zoos from latitudes 43 to 53°N and in different natural habitats; short-day (dark) and long-day (light) periods are indicated by sun symbols and the extent of day-length variation over the year in the different latitudes is indicated by the different amplitudes and colour graduations of these symbols (the greater the day length difference the greater the contrast between dark and light), calculated with the minimum gestation length: A) captive Asian elephants in zoos from latitudes 43 to 53°N; B) free-ranging Asian elephants, Mudumalai National Park (10.42°N), India, Sukumar et al. (1997); C) free-ranging Asian elephants, Udawalawe National Park (6.29°N), Sri Lanka, De Silva et al. (2013); D) captive African elephants in zoos from latitudes 43 to 53°N; E) free-ranging African elephants, Samburu National Reserves (0.61°N), Kenya, Rasmussen (2001); F) free-ranging African elephants, Amboseli National Park (2.65°S), Kenya, Moss (2011); G) free-ranging African elephants, Wankie National Park (18.45°S), Zimbabwe, Williamson (1976); H) free-ranging African elephants, Kruger National Park (23.99°S), South Africa, Smuts (1975)





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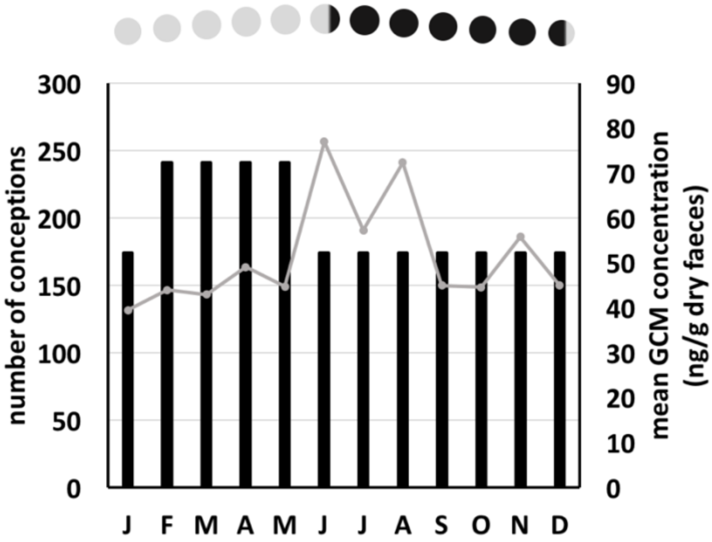
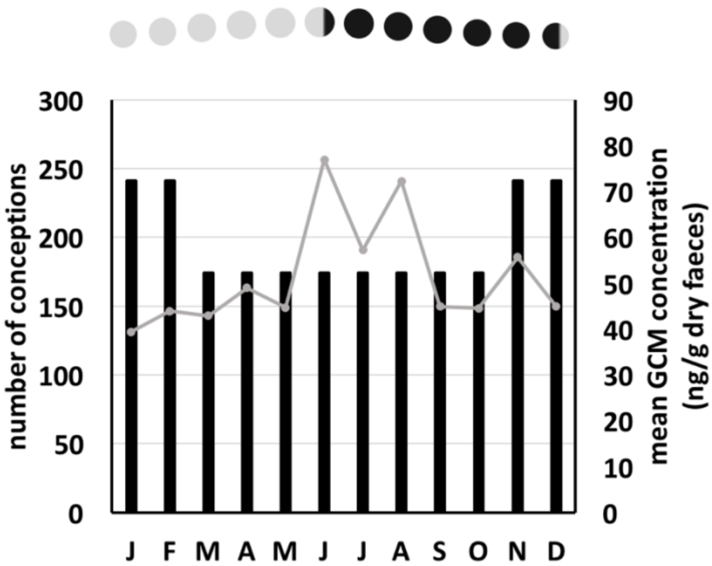


Figure S3 minimum Mean monthly glucocorticoid metabolite concentration (GCM) in faeces of female Asian elephants aged 17-55 years (N=37) from timber work camps in Myanmar (21.91°N; grey line) (Mumby et al. 2015a) and number of conceptions by month of timber elephants in Myanmar calculated with the minimum gestation length (black bars; Mumby et al. 2013; 41% of conceptions took place from Feb-May, N= 2350, average conceptions calculated for each month). Feb-May = rest time, Jun = start of working period and monsoon (Mar 2002). For meaning of sun symbols, see Fig. 2.



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